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BIOLOGY OF HYDRACTINIID HYDROIDS. 1. COLONY ONTOGENY IN *HYDRACTINIA ECHINATA* (FLEMMING)

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ABSTRACT

The colonial marine hydroid, *Hydractinia echinata,* exhibits a wide range of growth morphologies during ontogeny, from sheet-like colonies of uniform ectodermal mat to colonies which produce complex networks of stolons. Colony ontogeny was quantified under uniform environmental conditions for 70 colonies of *H. echinata,* with data collected on the growth rates of the three major colony parameters: mat tissue, stolon tissue, and polyps. Analysis of the relative growth rates of the tissues clearly illustrates that variability in colony form between colonies can be attributed to continuous variation in just one of the parameters governing colony ontogeny.

INTRODUCTION

Despite their phylogenetic and ecological diversity, the many colonial phyla share a limited number of general colony forms. Much recent work has focussed on the geometrical properties and mechanical constraints of particular morphologies (Riedl, 1971; Kaufman, 1973; Wainwright, *et al.,* 1976; Alexander, 1977; Jackson, 1979; Buss, 1979; Cheetham *et al.,* 1980, 1981 and many others). Mechanical constraints clearly limit the range of physical regimes suitable for occupation by a given morphological type. For instance, highly branched upright forms may not be able to withstand areas of strong water movement, where sheet-like forms of low vertical relief may thrive; calmer waters where arborescent forms are more abundant may not be suitable for sheet-like organisms due to higher rates of sedimentation. Likewise, one can infer varying degrees of susceptibility to biological threats from geometric considerations of different morphologies. For instance, a sheet-like organism, with a large surface area in contact with the substratum, may be more susceptible to a surface-bound predator or competitor than the arborescent form. Conversely, the tree-like organism may be more susceptible to a generalized water-column-dwelling predator than the sheet-like form. Several authors have attempted, with considerable success, to predict the distribution and abundance of various colonial organisms as a function of morphological type (Wainwright and Dillon, 1969; Kaufmann, 1973; Chamberlain and Graus, 1975; Wainwright and Koehl, 1976; Brakel, 1976; Winston, 1976; Graus, *et al.,* 1977; Chamberlain, 1978; Jokiel, 1978; Buss, 1979; Foster, 1979; Jackson, 1979, and many others).

Parallelling this ecological interest in patterns of gross colony morphology, there has been an increase in interest in the phyletic distribution and fossil record of different morphologies (Boardman and Cheetham, 1973; Thomsen, 1977; Chamberlain, 1978; Van Valen, 1978; Jackson, 1979; Larwood and Taylor, 1979; Cheetham, *et al.,* 1980,

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1981; Cheetham and Thomsen, 1981; Schopf *et al.*, 1981, and many others). Jackson (1979) noted that similar morphological trends have evolved repeatedly in distantly related groups, despite considerable differences in the physiological complexity of the organisms in question. Perhaps even more striking is the observation that the same set of morphological types reappear in a given lineage following episodes of extinction. The clear ecological significance of various morphologies, coupled with the extreme conservatism of these forms throughout geologic time, suggest that detailed examination of variation in growth morphology may ultimately yield useful insights into the mechanisms of evolutionary change.

In some species, individual colonies may exhibit very different patterns in growth (Toriumi, 1955; Oliver, 1968; Boardman and Cheetham, 1973; Brakel, 1976; Buss, 1979; Jackson, 1979, and many others), often to the point that they may mistakenly be classified as separate species (Wood-Jones, 1907). Species of variable morphology are of particular interest to evolutionary studies, as these species are assumed to possess the genetic architecture necessary for the adoption of alternative morphological types. Species which are capable of producing variable growth forms have some clear advantages over those which are limited to a single mode of growth. Morphological plasticity often implies ecological plasticity, and species which exhibit variable colony morphologies consequently should be distributed over a wider range of microenvironments. Not only do morphologically variable species possess wide environmental tolerances (Jackson, 1979), but several species also to alter their morphology as a function of environmental conditions such as temperature (Crowell, 1957; Bushnell, 1966; Tusov and Davis, 1971; Jebram, 1973), microstratigraphy (Bushnell, 1966; Barnes, 1973), and nutritional regime (Crowell, 1957; Fulton, 1962; Tusov and Davis, 1971; Jebram, 1973; Winston, 1976; Jebram and Rummert, 1978).

Despite the widespread appreciation of the importance of species of variable morphology, there has been little attempt to (a) quantify this variation, (b) demonstrate a genetic basis for this variation, or (c) determine the requisite developmental shifts required to generate this variation. Here we present the results of a 'common garden' experiment in which variation in the ontogeny of colonies of the athecate hydroid, *Hydractinia echinata,* was quantified under constant environmental conditions. Our results suggest a large genetic component to the observed variability. Furthermore, analysis of rates and interactions of the major parameters of colony growth suggests that complex developmental processes and major changes in form may be largely reflected in continuous variation of a single growth parameter.

Materials and Methods

Hydractinia echinata is an athecate colonial hydroid commonly found on gastropod shells inhabited by hermit crabs of the genus *Pagurus.* A mature colony consists of an encrusting, spinose basal mat from which several specialized zooid types arise; these include feeding polyps, reproductive polyps (blastostyles), and two specialized zooids of debatable function, the spiral zooids and the tentacular zooids. *Hydractinia echinata* is strictly dioecious and sex determination is likely under genetic control (Hauenschild, 1954). Sexual reproduction yields a planula larva which settles on a pagurid-occupied shell, metamorphoses into a feeding polyp, and then produces a colony by asexual iteration (Fig. 1).

Two different developmental processes regulate the growth of a *H. echinata* colony across a planar substratum: (1) expansion of basal mat and (2) elongation of stolons. Mat tissue is composed of a close network of entodermal gastrovascular canals surrounded by interstitial cells and covered by a uniform layer of ectoderm. Stolons are

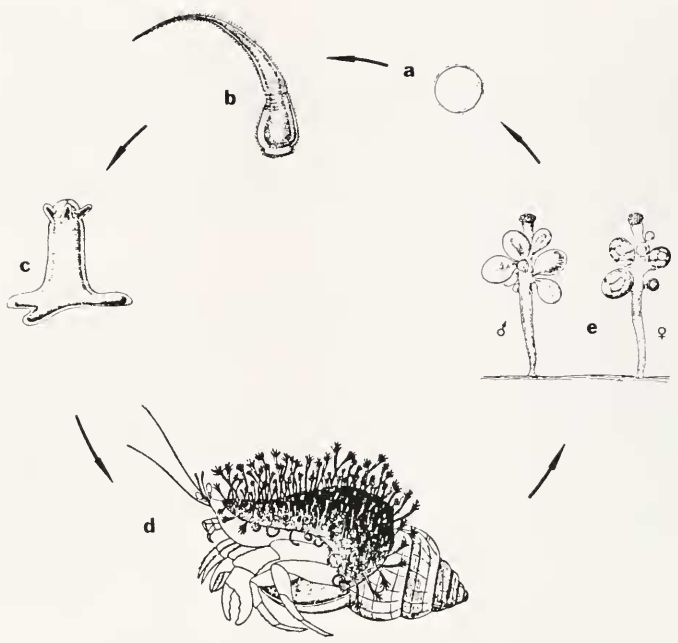

FIGURE 1. Life cycle of *Hydractinia echinata*. Fertilized egg (A) develops into crawling planuloid larva (B) which attaches to substrate and metamorphoses into a primary polyp (C). By asexual iteration this polyp develops into a mature colony (D) which will produce either male or female reproductive polyps (blastostyles) (E). (A modified from Benard-Boirard, 1962; B and C modified from Mueller, 1973; D and E modified from Hauenschild, 1954).

individual periderm-covered entodermal tubes which branch and anastomose with one another to form highly complex networks across the substrate. Feeding polyps arise from the mat tissue and, in some genotypes, from the stolon.

Although colony ontogeny has never been quantified, previous workers have recognized distinct morphological types (Schijfsma, 1939; Hauenschild, 1954). At one end of the morphological spectrum are "matty" colonies (Fig. 2A), which produce little or no stolons and grow as uniform sheets. At the opposite extreme are "viney" colonies (Fig. 2B), which produce a complex stolon network which cover the substratum much more rapidly than does a solid sheet of mat tissue. However, all viney colonies do produce some mat tissue, which eventually fills in between the pre-existing stolonal network. This difference in morphology occurs solely during colony ontogeny; on the spatially limited substrata they inhabit, all *H. echinata* colonies eventually form solid encrusting mats.

The relative rates of production of mat and stolon throughout ontogeny differ between colonies, producing a characteristic pattern in gross morphology for a given colony. We have endeavored to grow field-collected colonies under uniform environmental conditions in order to separate the genetic and environmental components of variation in growth morphology. The theory and practice of common garden experiments has been reviewed in detail elsewhere (Turesson, 1922; Clausen *et al.*, 1940). The use of field-collected colonies to assess the genetic component of variability is subject to two potential criticisms. Field-collected colonies may not be genetically uniform; genetically distinct colonies may have fused prior to collection, producing chimera individuals. This is unlikely in *H. echinata* for three reasons: (1) several

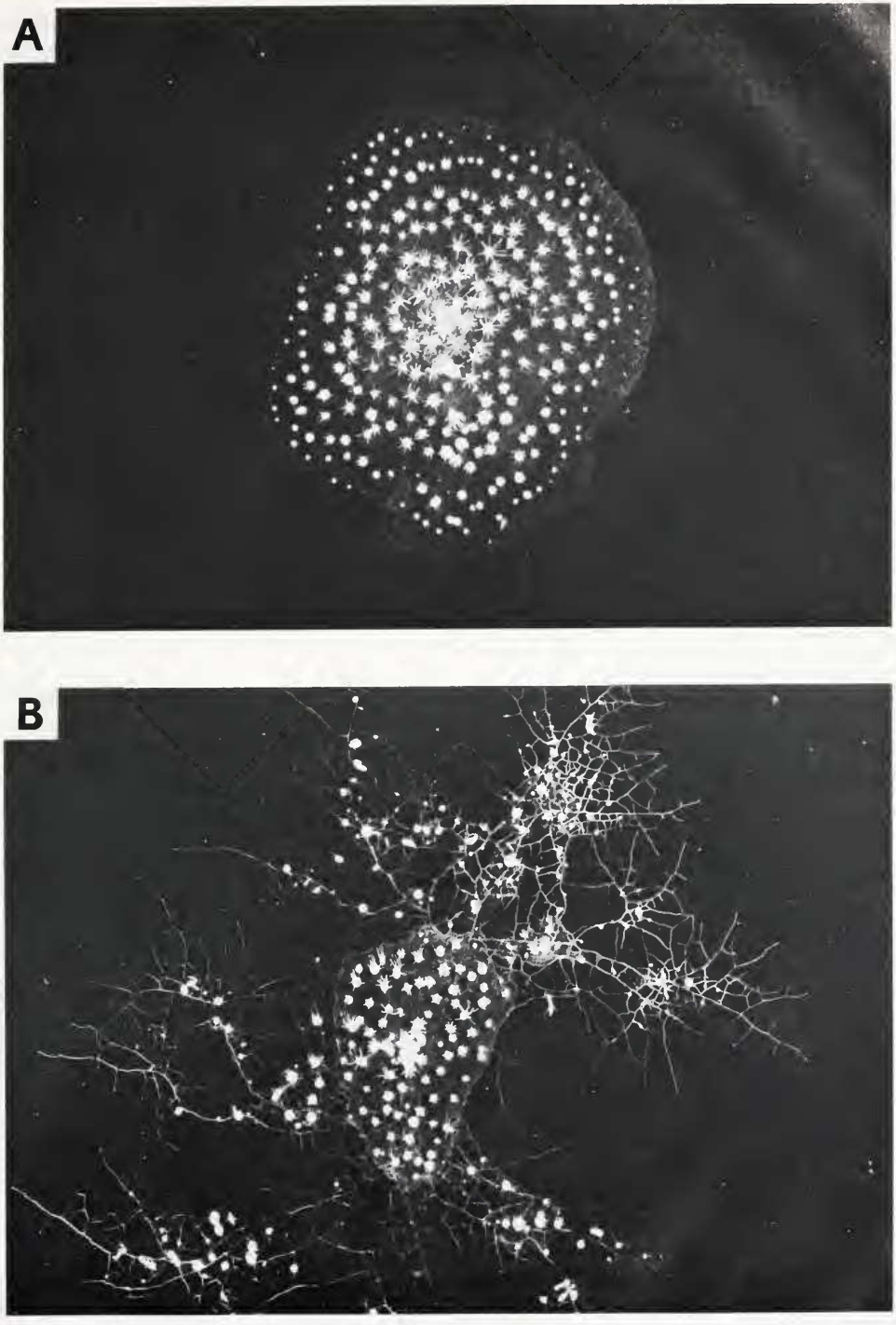

FIGURE 2. (A) A "matty" colony, which produces no stolons throughout colony ontogeny. (B) A "viney" colony, exhibiting a complex stolon network.

hundred attempted fusions between field-collected colonies have resulted in no cases of successful fusion, (2) studies of the genetics of fusibility in *H. echinata* demonstrate that fusion is limited exclusively to close kin (Hauenschild, 1954, 1956; Ivker, 1972; Buss and McFadden, unpubl. data), and (3) one-dimensional starch gel electrophoresis of 80 field-collected colonies failed to show evidence of multiple alleles for a given colony at a locus known to possess multiple alleles. The second caveat is that field-collected colonies may have been fixed in a constant morphology by some environmental factor which acted prior to the collection of the colonies. This is also unlikely for *H. echinata,* as colonies raised from planulae under constant conditions in the laboratory also display wide variability in growth morphology. Although there is no adequate substitute for quantitative genetic analysis to determine the genetic component of complex traits, the observation of wide variability in individuals cultured under constant conditions represents strong evidence for a genetic component to the observed variability.

The *H. echinata* colonies used in this study were collected from a shallow subtidal (−3 m), gravel bottom adjacent to No Man's Island, Old Quarry Harbor, Guilford, Connecticut. Using SCUBA, individuals of *Pagurus longicarpus* with hydroid-covered shells were collected haphazardly. Small pieces of basal mat containing 1–3 feeding polyps were removed from each shell with a scalpel; these explants were placed on black plexiglass culture slides, and gently held down by a loop of suture thread tied around the slide (Ivker, 1972). After 1–3 days explants had attached to slides and the threads were removed. These stock cultures were maintained in recirculating sea water at room temperature. They were fed for 2 hours daily with day-old brine shrimp nauplii, and the water changed immediately after each feeding. Food levels were sufficient to allow each colony to feed to repletion. Colonies were cleaned weekly with a small camel-hair brush to remove growth-inhibiting detritus from the surfaces of the substratum.

To initiate observations, explants of mat tissue containing three feeding polyps were excised from each of the stock colonies, and allowed to reattach to plexiglass slides in the manner described above. For each strain only one daughter colony was observed. This is justified on the basis of unpublished data which demonstrates that replicate explants removed from the same colony produce nearly identical patterns in colony ontogeny (Buss and Grosberg, in prep.). Beginning with its date of attachment to the slide, each colony was traced at approximately 4-day intervals, using a camera lucida attachment to a Wild M-5 dissecting microscope at 15×. After a period of three weeks the stolonal network of most colonies had become too extensive to conveniently trace. Thereafter, colonies were photographed at weekly intervals for another 8 weeks. To facilitate data analysis, photographs were converted to line drawings of mat area and stolons. Contact prints were placed under a dissecting microscope and traced at 7.5× using a camera lucida. These pencil drawings were then copied on a Kodak copier to yield high-contrast black-and-white representations of each drawing. Because of the time necessary to produce each drawing, not every photograph was analyzed; rather, a representative series of dates was chosen for each colony.

The cumulative growth of mat, stolon, and polyps was calculated for each colony. The number of polyps present in a colony on each date of observation was counted directly from the camera lucida tracing or contact print of the colony. The drawings of mat tissue were manually digitized on an Apple II minicomputer graphics tablet and the area of mat tissue present at each date of observation calculated. In a growing, pre-reproductive colony the mat tissue and feeding polyps are rarely resorbed, hence the area of mat tissue and the number of polyps actually present at each date of observation is equivalent to cumulative growth for both of these parameters.

Stolonal networks were analyzed using an image analysis system (Measuronics Corp., Linear Measuring Set [LMS]) to determine total length of stolon present at each date of observation. The LMS performs an analog to digital conversion on an image which has been projected onto a video screen. The LMS is interfaced with an Apple II minicomputer and utilizes software which counts pixels to compute the desired length measurements. Complex stolon networks were processed by direct video analysis to determine total length of stolon present. Simpler stolonal networks were manually digitized using the Apple graphics tablet and the stored images were subsequently processed with the LMS to obtain stolon length measurements.

Unlike mat and polyp tissue, the length of a stolon network on any given date is not equivalent to the cumulative growth of stolon, since stolons are continually being overgrown by mat tissue. To evaluate cumulative stolonal growth, camera lucida tracings made on successive dates of observation were overlaid such that the amount of stolon which was new at each date could be determined. Only the new stolons were digitized for each of the observation dates for which camera lucida tracings had originally been made. Cumulative growth was determined by summing the values of new growth for each date. New growth was more difficult to determine from the photographic data because the magnification at which the colonies were photographed decreased as the colonies grew, thus making direct overlay of successive dates difficult. In these cases, the entire stolon network present at a given date was digitized. The photograph was then compared to earlier photos of the colony. With few exceptions, it was possible to find an earlier photograph which could be compared with the later one such that the stolon networks appeared mutually exclusive (*i.e.*, no individual stolons appeared in both photographs, yet there was also no large gap of unrecorded stolon growth between the two observations). The length of stolon present at the later date was added to the cumulative growth of stolon at the earlier date to yield cumulative growth at the later date. Although these comparisons are less reliable than direct overlays of drawings made on successive dates, any errors introduced by this process were uniformly applied to all colonies and hence do not influence comparisons between colonies.

RESULTS

Of the 72 original explants, 70 (97.3%) reattached without difficulty and grew continuously until the project was terminated. For each of these colonies (39 male and 31 female) plots were made for the cumulative growth of mat area, polyp number, and stolon length *versus* time. Plots of two of the 70 strains are presented in Figures 3A and 3B. These correspond to the 'matty' and 'viney' colonies illustrated in Figures 2A and 2B. All growth data were fitted to 1st, 2nd, and 3rd order growth equations. As may be expected with data of this sort, no single growth equation proved ideal for all 70 colonies (Kaufmann, 1981). Accordingly, comparison between colonies were made on the basis of the simplest equation, a linear regression of the log-transformed data (log [mat, stolon, polyp] = m log [time]), calculated for each growth parameter for each colony (Table I). This approach allows one to compare a given parameter between colonies on the basis of a single statistic, the slope of a regression line with the intercept near zero (Kaufmann, 1981). The fits of the regression lines (Table I) were significant to at least the $P < 0.05$ level for mat and polyp growth for all colonies. Regressions of stolon length were significant to at least $P < 0.05$ in all but five cases. These few departures from linearity all represent colonies which exhibited a long period of no stolonal growth followed by a sudden production of stolon.

Pearson's product-moment correlation coefficients were determined to test for association between the slopes of the regression lines for each of the three parameters.

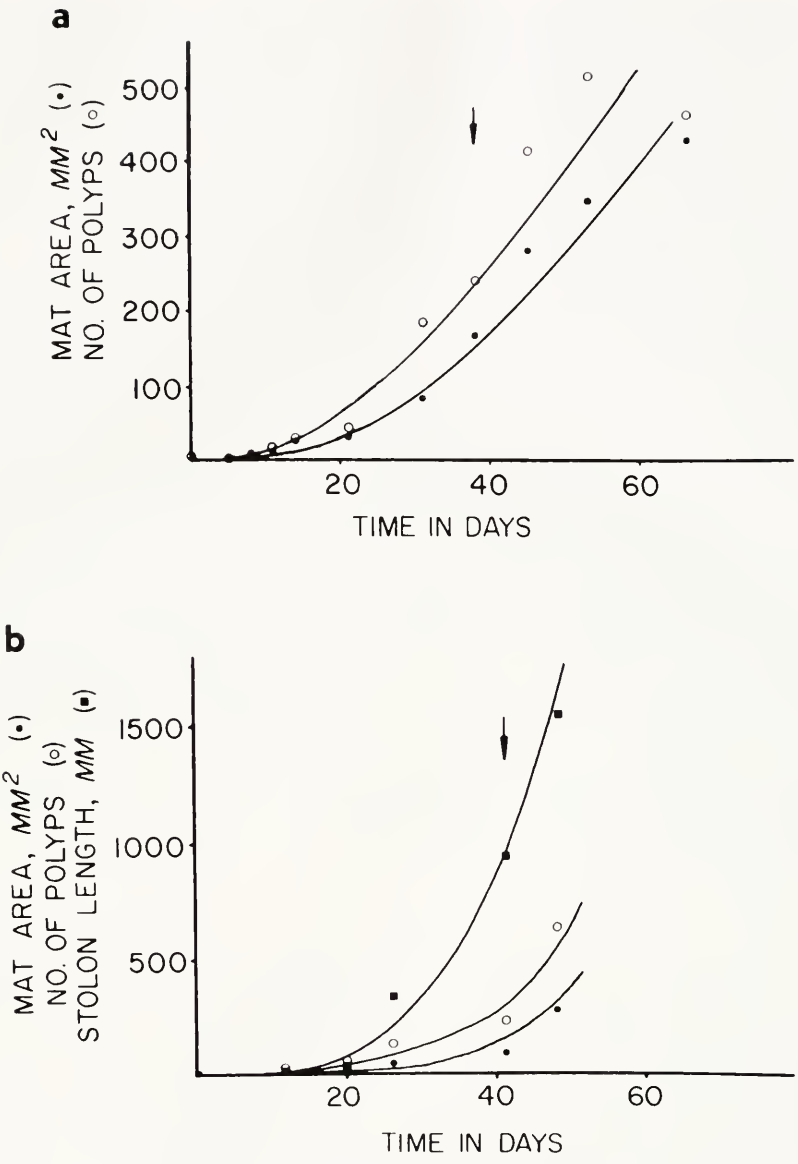

FIGURE 3. (A) Cumulative growth curves of mat tissue and polyps of colony 15, the matty colony shown in (2A). (B) Cumulative growth curves of mat tissue, polyps, and stolons of colony 141, shown in (2B). Arrows indicate date at which photograph was taken. Curves are fitted by hand.

Each slope value was weighted by the inverse of the variance of its regression to account for the differing confidence in the estimate of the slope for each growth curve. There is no significant association between the growth rates of mat and stolon ($s = -0.0559$, $P > 0.645$), nor is there any association between the growth rate of stolons and polyps ($s = 0.0839$, $P > 0.489$). There is, however, a significant association between the growth rates of mat and polyps ($s = 0.297$, $P = 0.012$). There are no

significant differences between the sexes in any of the three growth parameters (polyps: $F = 2.80$, $P > 0.098$; mat: $F = 0.67$, $P > 0.415$; stolon: $F = 0.03$, $P > 0.085$).

A cluster analysis (SAS statistical package) was performed on the growth rates to determine if the colonies could be segregated into different groups based on the values of growth rates of mat, stolon, and polyps characterizing each colony. Two different groups are present (Table I), which are separated by a distance ratio of 0.715 (number of distances within cluster: total number of distances). These two clusters represent matty ($n = 15$) and viney ($n = 55$) colonies (Fig. 4). The growth rates of neither mat ($F = 1.27$, $P > 0.264$) nor polyps ($F = 0.85$, $P > 0.358$) differed between the two clusters. The only significant difference between these groups was in the growth rate of stolon tissue ($F = 4.34$, $P = 0.041$).

The ontogeny of a colony of *H. echinata* is an expression of the manner in which energy derived from feeding polyps is allocated to the production of mat and stolonal tissues. Our results demonstrate (1) that variation in colony morphology is maintained under constant culture conditions, implying a large genetic component to observed variation, (2) that the variation is unrelated to colony sex, and (3) that most variation is not a result of differential allocation of resources to both mat and stolon production, rather that it is largely the difference in the rate of growth of stolonal tissue which gives rise to the wide spectrum of colony growth morphologies exhibited by *H. echinata.*

Discussion

The patterns in ecological distribution and evolutionary history of various colonial growth morphologies yield a variety of predictions as to environmental and phylogenetic distribution, but tell us little about the mechanisms which generate colony form and the relative ease or difficulty in generating changes in this morphology. The form of any colony may be dissected into a number of observable growth parameters. Each parameter, however, is the result of a complex series of morphogenetic events. Ultimately, observable growth parameters must be understood in terms of the underlying genetic organization controlling both the expression of various developmental processes and the rate at which this expression is realized.

In the absence of this information, several investigators have developed simulation models directed at determination of the extent of change necessary to generate variation in observable growth parameters. This approach in colonial invertebrates has been pioneered by Braverman (Braverman and Schrandt, 1966; Braverman, 1974). Using a series of computer simulations he demonstrated that very complex developmental patterns can be generated by the recursive application of simple, probabilistic rules of growth to an environment which is consecutively changed only by the previous application of the same rules. By specifying simple rules of growth for each of the three parameters of colony ontogeny (*i.e.,* growth of stolon, stolon branching frequency, and number of polyps), Braverman and Schrandt (1966) were able to produce a computer-generated model of a colony of *Podocoryne carnea* which roughly approximated the observed growth morphology of this hydractiniid hydroid.

Computer generated patterns which approximate actual biological patterns are of considerable interest and have been developed for a variety of other systems (*e.g.,* tree and rhizomatous plant morphology: Kamiya and Togawa, 1972; McMahon, 1975; Fisher and Honda, 1977; Niklas, 1978; Halle and Tomlinson, 1978; Bell and Tomlinson, 1980, and many others). These models illustrate that seemingly complex morphological shifts may be the result of the recursive application of a very small number of changes in basic rules. The implication is that in biological systems genes may be construed as rules which direct development and the phenotype may be

TABLE I

Hydractinia echinata *colony ontogeny*

Colony	N	Slope of mat growth curve	r^2	Signif.*	Slope of polyp growth curve	r^2	Signif.*	Slope of stolon growth curve	r^2	Signif.*	Cluster	Sex
1	8	0.996	.83	$P < .01$	0.918	.87	$P < .001$	1.038	.98	$P < .001$	2	M
3	8	1.906	.99	$P < .001$	1.579	.90	$P < .001$	0.439	.47	NS	1	M
4	10	1.821	.89	$P < .001$	1.187	.89	$P < .001$	1.238	.91	$P < .001$	2	M
5	8	1.030	.77	$P < .01$	0.851	.65	$P < .05$	1.395	.42	NS	2	M
6	9	1.588	.94	$P < .001$	1.439	.93	$P < .001$	1.783	.99	$P < .001$	2	M
7	7	1.530	.85	$P < .01$	1.561	.97	$P < .001$	0.954	.87	$P < .01$	2	M
8	7	1.549	.93	$P < .001$	1.319	.77	$P < .01$	1.920	.92	$P < .001$	2	M
9	7	1.273	.90	$P < .01$	1.231	.90	$P < .01$	1.016	.94	$P < .001$	2	M
10	9	1.887	.90	$P < .001$	1.408	.94	$P < .001$	1.323	.98	$P < .001$	2	M
11	6	1.567	.95	$P < .001$	1.000	.80	$P < .05$	0.839	.99	$P < .001$	2	M
13	11	1.582	.84	$P < .001$	1.191	.83	$P < .001$	1.678	.82	$P < .001$	1	M
14	11	1.518	.99	$P < .001$	1.307	.92	$P < .001$	0.857	.34	NS	2	M
15	11	1.538	.95	$P < .001$	1.511	.92	$P < .001$	0.00	.00	NS	1	M
16	9	1.678	.72	$P < .01$	1.413	.74	$P < .01$	2.106	.68	$P < .01$	2	M
17	12	1.155	.92	$P < .001$	0.806	.86	$P < .001$	0.669	.51	$P < .05$	1	M
18	10	1.684	.94	$P < .001$	1.206	.93	$P < .001$	1.488	.96	$P < .001$	2	M
19	11	1.702	.86	$P < .001$	1.368	.90	$P < .001$	1.731	.91	$P < .001$	2	M
20	9	1.567	.94	$P < .001$	1.225	.80	$P < .01$	2.060	.92	$P < .001$	2	M
21	7	1.428	.92	$P < .001$	1.198	.90	$P < .01$	1.490	.52	NS	2	M
24	8	1.405	.94	$P < .001$	1.098	.91	$P < .001$	1.432	.99	$P < .001$	2	M
26	9	1.475	.86	$P < .001$	1.027	.85	$P < .001$	1.218	.93	$P < .001$	2	M
27	11	2.231	.90	$P < .001$	1.559	.84	$P < .001$	1.484	.89	$P < .001$	2	M
28	11	1.482	.94	$P < .001$	1.137	.86	$P < .001$	1.587	.98	$P < .001$	2	M
29	9	1.378	.88	$P < .001$	1.066	.78	$P < .01$	0.198	.32	NS	1	M
30	7	1.994	.95	$P < .001$	1.675	.94	$P < .001$	1.977	.85	$P < .01$	2	M
31	11	1.940	.93	$P < .001$	1.532	.85	$P < .001$	2.087	.79	$P < .001$	2	M
32	3	1.380	.97	$P < .001$	1.177	.84	$P < .01$	1.123	.63	$P < .05$	2	M
33	9	1.228	.94	$P < .001$	1.035	.92	$P < .001$	0.729	.91	$P < .001$	1	M
34	10	1.412	.91	$P < .001$	1.318	.85	$P < .001$	0.00	.00	NS	1	M
35	6	1.374	.95	$P < .001$	1.064	.96	$P < .01$	0.841	.99	$P < .001$	1	M
36	10	1.404	.77	$P < .001$	1.073	.89	$P < .001$	1.601	.98	$P < .001$	2	M
37	7	1.102	.94	$P < .001$	1.049	.92	$P < .001$	1.134	.96	$P < .001$	2	M

38	9	1.260	.93	$P < .001$	1.358	.92	$P < .001$	1.968	.94	$P < .001$	2	F
40	9	1.046	.94	$P < .001$	1.042	.91	$P < .001$	0.999	.47	$P < .05$	2	F
41	9	0.946	.96	$P < .001$	0.565	.79	$P < .01$	0.00	.00	NS	1	F
42	11	1.895	.92	$P < .001$	1.383	.94	$P < .001$	1.096	.95	$P < .001$	2	F
43	10	1.329	.95	$P < .001$	1.284	.93	$P < .001$	1.369	.99	$P < .001$	2	F
101	7	1.028	.83	$P < .01$	0.494	.80	$P < .01$	0.760	.95	$P < .001$	1	F
102	9	1.704	.77	$P < .01$	1.389	.78	$P < .01$	0.872	.93	$P < .001$	2	F
103	7	1.416	.95	$p < .001$	1.049	.88	$P < .01$	1.086	.98	$P < .001$	2	F
106	8	1.251	.93	$P < .001$	1.124	.94	$P < .001$	0.933	.80	$P < .01$	2	F
107	7	1.646	.99	$P < .001$	0.879	.94	$P < .001$	1.305	.97	$P < .001$	2	F
108	8	1.616	.73	$P < .01$	1.121	.64	$P < .05$	1.640	.77	$P < .01$	2	F
110	11	1.473	.95	$P < .001$	1.079	.91	$P < .001$	0.700	.90	$P < .001$	1	F
111	8	1.450	.85	$P < .01$	1.182	.79	$P < .01$	1.165	.87	$P < .001$	2	F
112	6	1.699	.93	$P < .01$	0.404	.69	$P < .05$	0.733	.97	$P < .001$	1	F
114	6	1.784	.88	$P < .01$	1.304	.84	$P < .05$	1.702	.87	$P < .01$	2	F
115	7	1.294	.93	$P < .001$	1.245	.86	$P < .01$	1.894	.88	$P < .01$	2	F
116	10	1.692	.83	$P < .001$	1.277	.80	$P < .001$	1.333	.96	$P < .001$	2	F
117	7	1.561	.97	$P < .001$	1.225	.98	$P < .001$	1.478	.69	$P < .05$	2	F
119	5	1.125	.65	NS	1.062	.73	NS	1.936	.78	NS	2	F
121	9	1.469	.99	$P < .001$	1.041	.90	$P < .001$	0.568	.55	$P < .05$	2	F
123	6	1.097	.95	$P < .01$	0.733	.80	$P < .05$	0.00	.00	NS	1	F
125	9	1.741	.92	$P < .001$	1.682	.93	$P < .001$	1.734	.96	$P < .001$	2	F
126	9	1.709	.85	$P < .001$	0.744	.98	$P < .001$	1.650	.98	$P < .001$	2	F
127	9	1.328	.99	$P < .001$	0.769	.99	$P < .001$	1.614	.95	$P < .001$	2	F
129	6	1.495	.88	$P < .01$	1.313	.82	$P < .05$	1.619	.97	$P < .001$	2	F
130	9	1.269	.94	$P < .001$	1.283	.93	$P < .001$	1.263	.74	$P < .01$	2	F
131	10	1.608	.91	$P < .001$	1.236	.80	$P < .001$	1.551	.64	$P < .01$	2	F
133	8	0.971	.88	$P < .001$	0.922	.85	$P < .01$	1.522	.68	$P < .01$	2	M
134	11	1.528	.93	$P < .001$	1.279	.93	$P < .001$	0.00	.00	NS	1	F
135	8	0.852	.81	$P < .01$	0.932	.85	$P < .01$	1.524	.95	$P < .001$	2	F
136	5	1.536	.80	$P < .05$	1.433	.66	NS	1.644	.89	$P < .05$	2	F
138	7	1.008	.82	$P < .01$	0.923	.77	$P < .01$	1.316	.86	$P < .001$	2	F
139	6	1.516	.97	$P < .001$	1.172	.94	$P < .01$	1.277	.74	$P < .05$	2	F
140	9	1.673	.92	$P < .001$	1.108	.91	$P < .001$	1.349	.96	$P < .001$	2	F
141	8	1.564	.91	$P < .001$	1.305	.88	$P < .001$	1.886	.99	$P < .001$	2	F
A	7	1.051	.83	$P < .01$	1.071	.93	$P < .001$	1.757	.97	$P < .001$	2	M
B	7	1.283	.98	$P < .001$	1.113	.95	$P < .001$	1.215	.99	$P < .001$	2	M
D	6	1.166	.90	$P < .01$	1.254	.89	$P < .01$	1.854	.74	$P < .05$	2	F

* F-Statistic, one-tailed values, df = (1, N-1).

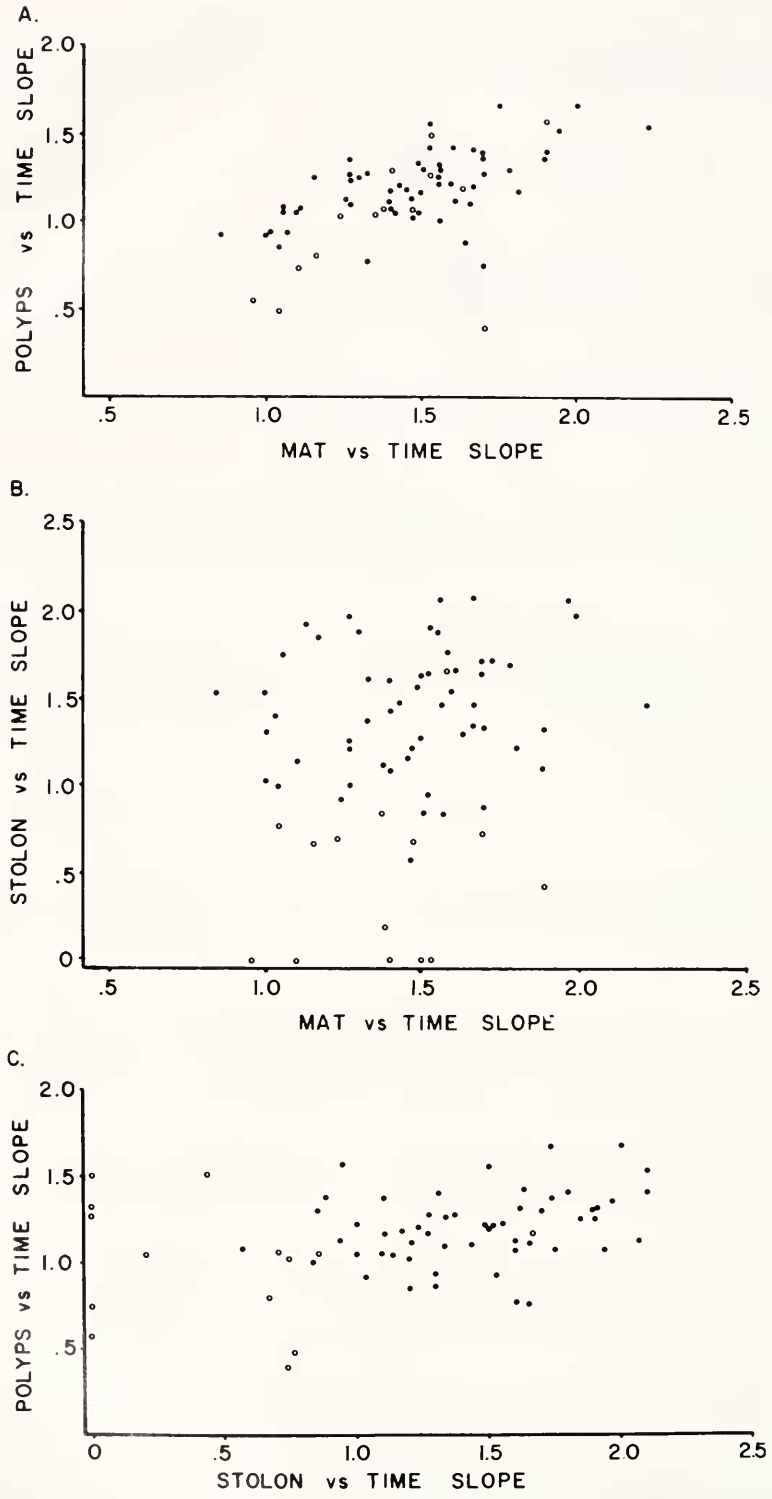

FIGURE 4. Scatter plots of the slopes of the regression lines for all 70 colonies, showing the two groups recognized by cluster analysis. (A) Mat growth rate *versus* polyp growth rate. (B) Mat growth rate *versus* stolon growth rate. (C) Stolon growth rate *versus* polyp growth rate. Open circles represent cluster 1, matty colonies. Closed circles represent cluster 2, viney colonies.

viewed as the end-product of the continuous application of a simple genetic instruction. A relatively minor change (*e.g.*, mutation or other genomic alteration) in a recursively applied rule (*e.g.*, gene) may result in a very different final product (*e.g.*, phenotype).

Although both computer modelling (Braverman and Schrandt, 1966) and geometrical treatments (Jackson, 1979) have suggested that major changes in form can be a result of variation in but a single parameter of growth, in no colonial organism with naturally-occurring variation in form has this been conclusively demonstrated. We have shown this to be the case in *H. echinata:* variation in gross colony morphology from uniform sheets to complex stolonal networks is largely controlled by variation in the rate of stolon production. Although more subtle distinctions between *H. echinata* colonies could likely be recognized by consideration of other growth parameters (*e.g.*, the branching frequency of stolons), our results clearly illustrate that large scale patterns in variability in colony form between colonies can be attributed to continuous variation in just one of the parameters governing colony ontogeny.

Models which predict that complex developmental patterns are controlled by recursive application of relatively simple rules, and that major changes in pattern consequently result from variation at a level far removed from the final phenotype are by no means tested by our data. Despite their enormous heuristic value, models of this sort are not without difficulty. Many different combinations of simple rules may yield essentially similar patterns and the actual mechanisms governing the growth of a hydroid colony can not be directly inferred from such models (Braverman and Schrandt, 1966). This problem underscores the fact that our knowledge of the manner in which eucaryote differentiation is determined has yet to have reached the stage at which the assumption of 'genes as rules' may be accepted as anything more than a working hypothesis. It is, however, this very uncertainty that makes the observation that variation in one component of the ontogenetic process has large-scale phenotypic consequences a matter of considerable interest.

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